Bacteria-Phage Antagonistic Coevolution in Soil

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Bacteria-Phage Antagonistic Coevolution in Soil

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Bacteria and their viruses (phages) undergo rapid coevolution in test tubes, but the relevance to natural environments is unclear. By using a "mark-recapture" approach, we showed rapid coevolution of bacteria and phages in a soil community. Unlike coevolution in vitro, which is characterized by increases in infectivity and resistance through time (arms race dynamics), coevolution in soil resulted in hosts more resistant to their contemporary than past and future parasites (fluctuating selection dynamics). Fluctuating selection dynamics, which can potentially continue indefinitely, can be explained by fitness costs constraining the evolution of high levels of resistance in soil. These results suggest that rapid coevolution between bacteria and phage is likely to play a key role in structuring natural microbial communities.

Host-parasite antagonistic coevolution—the reciprocal evolution of host defense and parasite counter-defense—is theoretically crucial to a range of ecological and evolutionary processes, including population dynamics and extinction risk, the evolution of diversity and speciation, the evolution of sex and mutation rates, and the evolutionary ecology of pathogen virulence (*1*–*4*). A number of excellent studies have inferred the operation of host-parasite coevolution in natural populations from patterns of local adaptation of parasites to their hosts in space and time (*5*–*10*). However, genetic variation between the host populations in space and time may be driven by parasite-imposed selection but could equally be driven by neutral process or additional selection pressures. A direct demonstration of coevolution requires evidence of host adaptation to parasites as well as parasite adaptation to hosts.

Antagonistic coevolution between bacteria and their ubiquitous parasites, bacteriophage (phage), is likely to be of particularly broad importance because of their extremely rapid rates of evolution (*3*, *11*)—the key role played by bacteria in ecosystem functioning—and the therapeutic use of phages as "evolving" antibiotics in agricultural and clinical contexts (*11*). Both the dynamics and consequences of coevolution between bacteria and viruses have been extensively studied in the laboratory (*12*, *13*), but little is known about the extent or role of rapid bacteria-phage coevolution in natural populations (*14*, *15*). Given that phages are typically highly specific to bacteria species and even genotypes (*11*) and the massive amount of diversity present in microbial communities (*16*), a given interacting bacteria and phage population is likely to make up a tiny fraction of the microbial community. It is therefore unclear whether phages, which only encounter hosts passively, impose sufficient selection on bacteria for rapid coevolution to occur.

We used a "mark-recapture" approach (*17*) to follow the ecological and evolutionary dynamics of a soil bacteria clone, *Pseudomonas fluorescens* SBW25, and a naturally associated lytic bacteriophage clone SBW25ϕ2 (*18*) in soil microcosms. Despite these organisms having been used extensively for in vitro evolution studies (*13*), they were frozen shortly after their original isolation and hence would have undergone little laboratory adaptation before our experiment. The

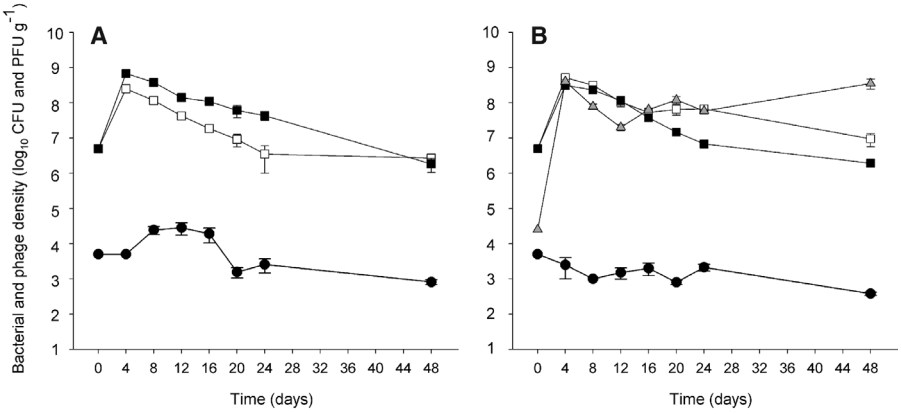

Fig. 1. Population dynamics of the bacterial and phage populations. Connected symbols show densities through time [mean $\log_{10}$(colony forming units/g soil) for bacteria or $\log_{10}$(plaque forming units/g soil) for phage, ± SEM] of phage SBW25ϕ2 (●); *P. fluorescens* SBW25 evolved in the presence (■) or absence (□) of phage; and the culturable fraction of the natural community (▲). Populations were evolved in the (**A**) absence and (**B**) presence of the natural community.

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phage, which is infectious to SBW25, can only be transmitted by lysis of the bacterial cell, resulting in the reciprocal evolution of resistant bacteria and infectious phages in nutrient media (*18*). Having established that no culturable bacteria in our soil were resistant to the antibiotic gentamicin (or could be infected by the experimental phage), we used an engineered gentamicin-resistant strain of *P. fluorescens* SBW25 (*3*) to inoculate the soil microcosms. All recovered bacteria that could grow on gentamicin therefore descended from the inoculated ancestral population. Similarly, we established that there were no phages in the soil that were able to infect *P. fluorescens* SBW25; hence, all recovered phages that could infect *P. fluorescens* SBW25 descended from the inoculated phage population. In an attempt to disentangle effects of the physical and biotic components of the soil environment, we cultured our bacteria and phage in sterilized soil, in which the resident microbial community had been reinoculated in some replicate communities but not in others. Samples from the replicate soil communities (eight per treatment combination) were collected every 4 days for 24 days, with a further sample taken after 48 days. At each time point, we determined densities and resistance and infectivity of the focal bacteria and phage, as well as densities of the culturable component of the total bacterial community, by plating onto antibiotic-free agar.

Phages reduced the mean density of the *P. fluorescens* population in the presence of the natural community, whereas in the absence of the natural community phages actually increased mean *P. fluorescens* density (generalized linear mixed model, interaction between presence/absence of natural community and phages: $F_{1,28} = 60$, $P < 0.0001$) (Fig. 1). In cases in which both bacteria and phages were co-inoculated, the presence of the natural community significantly reduced densities of bacteria ($F_{1,14} = 23.5$, $P < 0.001$) and phages ($F_{1,14} = 132.4$, $P < 0.001$) (Fig. 1B). The density-increasing effect of phages in the absence of the natural community is surprising, and its potential implications for the therapeutic use of phages warrants extensive future investigation. However, we speculated that phages selectively killed growing and not stationary cells (*19*), and the presence of high frequencies of growing cells [growth advantage in stationary phase (GASP) mutants] under nutrient limitation reduced population sizes (*20*). In contrast, selective elimination of growing *P. fluorescens* cells by phages did not increase *P. fluorescens* density in the presence of the natural community because this community also inevitably contained growing cells of different species.

Coevolution between this bacteria and phage in laboratory media typically results in the evolution of increased resistance and infectivity ranges through time (arms race dynamics) (*13*). Specifically, bacteria are more resistant to past than contemporary phages and more resistant to contemporary than future phages (*13*, *21*); the same pattern holds for phage infectivity. To determine whether this coevolutionary dynamic occurred in soil, we measured the infectivity to bacteria isolated from day 24 of ancestral (day 0) phages (past) and phages isolated from days 24 (contemporary) and 48 (future) within each replicate. Similarly, we measured the resistance of ancestral (day 0) bacteria (past) and bacteria from days 24 (contemporary) and 48 (future) to phages from day 24. In contrast to results in laboratory media, bacteria were more resistant to their contemporary than past and future phages (Friedman test of effect of time, with replicate fitted as a blocking factor: $P < 0.01$; $n = 16$ populations) (Fig. 2, A and B), and phages were least infective to contemporary than past and future bacteria ($P < 0.01$; $n = 16$ populations) (Fig. 2, C and D), with no effect of the presence of the natural community on resistance/infectivity patterns (Mann-Whitney tests: $P > 0.2$ for resistance/infectivity at each time point, and changes in time). This significantly greater resistance of bacteria to contemporary than to noncontemporary phages (and corresponding lower infectivity of phages) held when comparisons were made only between days 24 and 48 (Wilcoxon paired sample test: $P = 0.02$; $n = 16$ populations). We extended our measurements to all sampled time points and found the frequency of bacteria resistant to the ancestral (time zero) and contemporary phages to be approximately 2 and 10%, respectively (paired t tests of resistance to contemporary versus ancestral phages, averaged through time: $t = 3.5$, $P < 0.01$; $t = 10.2$, $P < 0.001$, $n = 16$ populations, for absence and presence of natural community, respectively) (Fig. 3), with the difference in resistance to contemporary and ancestral phages greater for populations evolved in the presence of the natural community (independent sample t test: $t = 6.0$, $P < 0.01$, $n = 16$ populations). Taken together, these results demonstrate that bacteria and phage rapidly evolve, but that they are not undergoing arms race coevolution.

The data are, however, consistent with coevolution in which parasite genotypes specialize on host genotypes, and fitness of a given genotype fluctuates through time (fluctuating selection dynamics) (*2*, *5*, *6*). If parasites adapt more rapidly than do hosts, fluctuating selection dynamics are on average expected to result in parasites better adapted to their contemporary compared with past and future hosts, and vice versa if hosts adapt more rapidly than do parasites (*6*). Our data show the latter pattern, unequivocally demon-

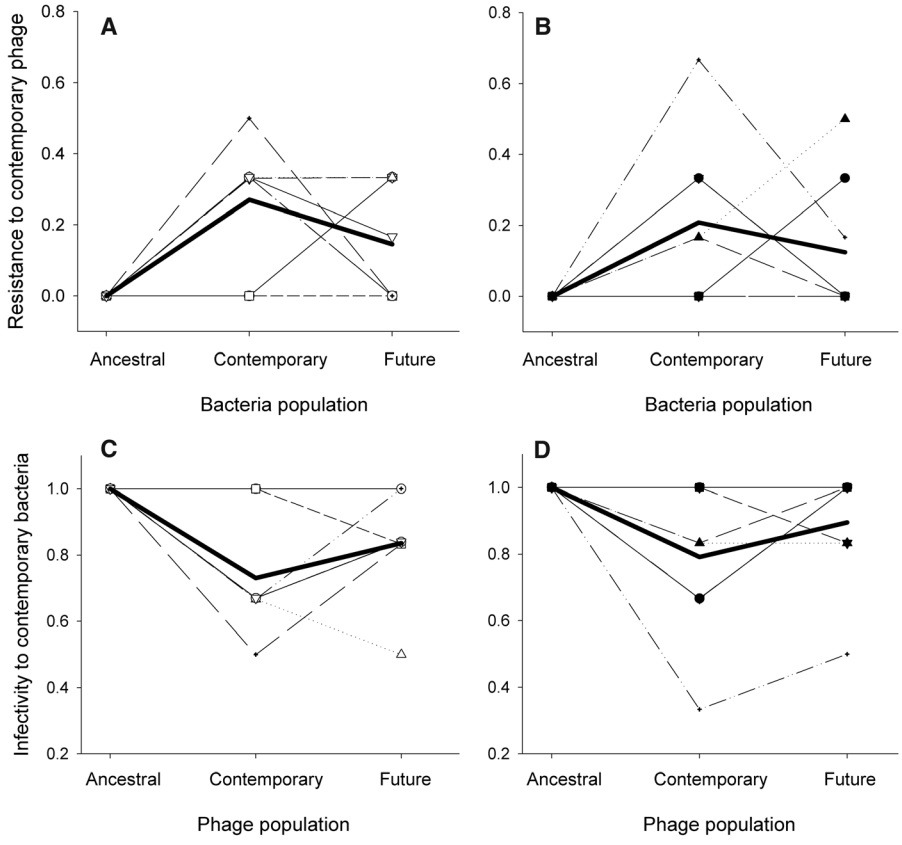

Fig. 2. Coevolutionary dynamics of bacteria and phages. Proportion of *P. fluorescens* isolated from day 24 resistant to ancestral (day 0) phage, contemporary (day 24), and future (day 48) phage populations evolved in the (**A**) absence and (**B**) presence of the natural community. Proportion of ancestral (day 0), day 24, and day 48 *P. fluorescens* susceptible to day 24 phages evolved in the (**C**) absence and (**D**) presence of the natural community. Individual thin lines indicate the eight separate replicates in each treatment; bold lines indicate means for all populations.

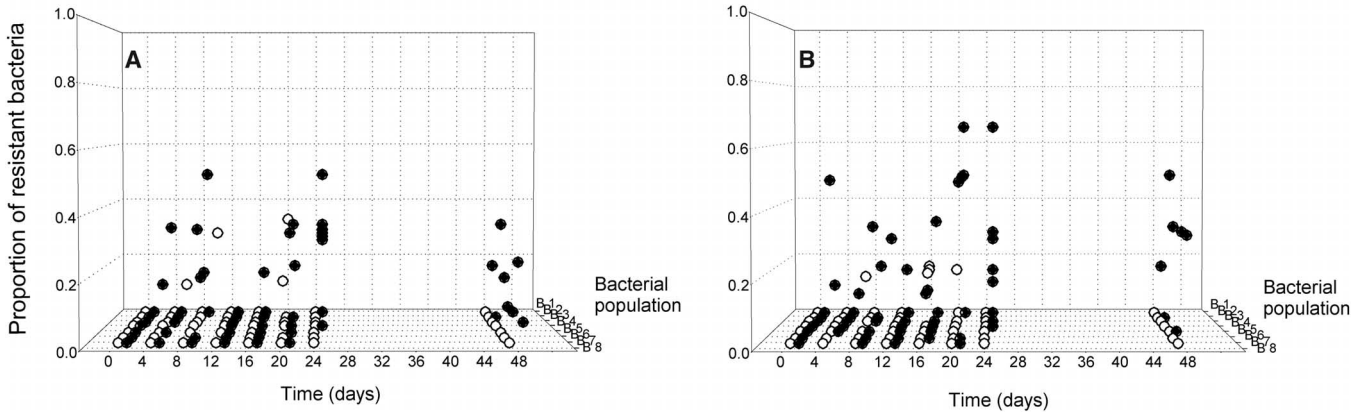

Fig. 3. Resistance of bacteria to ancestral and contemporary phages. Proportion of *P. fluorescens* resistant to the common ancestral (day 0) (○) and contemporary (●) phage populations evolved in the (**A**) absence and (**B**) presence of the natural community for all populations through time. No resistance to phages was detected in *P. fluorescens* populations evolved in the absence of phages.

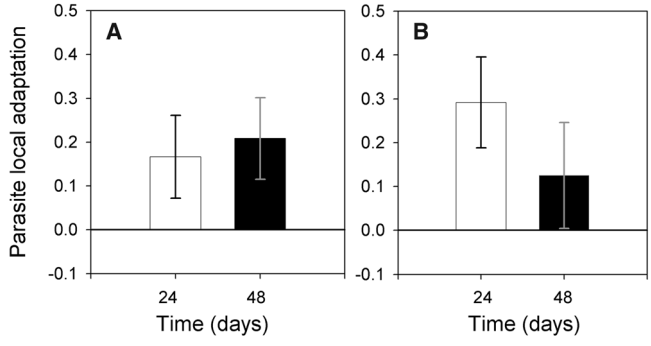

Fig. 4. Phase local adaptation. Mean local adaptation (proportion of local to foreign clones of bacteria susceptible to local phages) ± SEM measured at days 24 and 48 in the (**A**) absence and (**B**) presence of the natural community.

strating adaptation of bacteria populations to the evolving phage populations. Phages require susceptible hosts to propagate; hence, it is almost certain that evolutionary changes in phage infectivity also result from adaptation to evolving hosts. The operation of fluctuating selection dynamics is important because this type of coevolution can potentially continue indefinitely and maintain genetic diversity within populations (*2*), whereas arms race dynamics purge diversity and require a continual supply of novel mutations, so may be short-lived.

In an attempt to obtain more direct evidence of phage adaptation to evolving bacteria, we measured interactions between bacteria and phages in space as well as time by comparing the infectivity of phages to their local bacteria with infectivity to bacteria from replicate microcosms. We found that phages were significantly locally adapted, performing consistently better on local as compared with foreign bacteria (paired *t* test of infectivity to local versus foreign phages, averaged through time: $t = 3.4$, $P < 0.01$, $n = 16$ populations) (Fig. 4), with no difference between communities evolved in the presence or absence of natural communities (*t* test: $P > 0.2$). These data unequivocally demonstrate that phages adapt to changes in bacterial resistance.

Consistent local adaptation in space is commonly used to infer greater rates of adaptation of one evolving partner over the other in putative coevolutionary interactions (*22*, *23*). Our spatial data would therefore suggest phages adapt more rapidly than do bacteria. However, this interpretation is in apparent contrast to the direct measurements of adaptation in time, which suggest that bacteria adapt more rapidly than do phages. These results suggest that host-parasite adaptation in space and time need not be positively correlated (*6*) and that local adaptation in space may tell us little about relative rates of adaptation.

Despite direct evidence for bacteria-phage coevolution in soil, the fluctuating coevolutionary dynamics are markedly different from the arms race dynamics observed in high-nutrient broth, in which bacteria and phages with increasingly broad resistance and infectivity ranges, respectively, are favored through time. What limits the evolution of bacterial resistance and phage infectivity in soil, resulting in the change from arms race dynamics in vitro to fluctuating selection dynamics in soil? Theory suggests that growth-rate costs associated with resistance and infectivity might be important (*24*, *25*), and there is evidence for bacteria bearing costs of resistance to phage (*26*, *27*), and that these costs are greater in less productive environments (*28*). We therefore hypothesized that resistance was more costly in soil, which typically supports lower microbial biomass than does high-nutrient media. To test this hypothesis, we examined the competitive ability (relative to ancestral bacteria) of soil-evolved phage-resistant and -sensitive clones of bacteria in both broth and soil environments in the absence of phages. After competing for 2 days in high-nutrient broth in the absence of phages, no competitive costs associated with resistance were detected [(generalized linear model (GLM), phage-resistant versus -sensitive clones: $P > 0.2$) (fig. S1). In contrast, there was an approximately 36% reduction in relative fitness associated with resistance in soil (GLM, phage-resistant versus sensitive clones: $F_{1,21} = 7.6$, $P = 0.01$) (fig. S1), which did not differ between resistant clones that had evolved in the presence and absence of the natural community (presence versus absence of natural community: $P > 0.2$) (fig. S1). The costs associated with phage resistance in soil may explain why the evolution of resistance in soil is limited to co-occurring phages rather than to a wide range of previously encountered phage populations observed during coevolution in nutrient broth (*18*).

Despite considerable differences between the population dynamics of the focal bacteria and phages in the presence versus the absence of the natural microbial community, coevolutionary dynamics were very similar. There was no difference in the magnitude of parasite local adaptation in space (Fig. 4) and only small differences in patterns of adaptation in time, with an approximately 4% greater resistance to contemporary phages in the presence of the natural community (Fig. 3). If anything, we expected weaker selection for resistance, and less coevolution, in the presence compared with absence of the natural community, in part because of the reduced densities of the focal bacteria and phages (Fig. 1) (*28*). The limited impact of the microbial community on coevolution suggests that intraspecific competition and parasitism play a more substantial role than interspecific competition in driving evolution within microbial soil communities.

Our results show that bacteria and phage rapidly coevolve in soil, with very similar dynamics in the presence and absence of the natural

microbial community. Coevolution altered ecological population dynamics and resulted in bacteria adapted to phages in time and phages adapted to bacteria in space. Unlike coevolution in high-nutrient broth, coevolutionary dynamics in soil appear to be driven by fluctuating selection—a form of coevolution that can potentially continue indefinitely. These results suggest that rapid bacteria-phage coevolution, and not just purely ecological interactions, are likely to be crucial in explaining the structure, population dynamics, and ultimately the function of natural microbial communities.

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References

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Differences in Thermal Tolerance Among Sockeye Salmon Populations

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Climate change–induced increases in summer water temperature have been associated with elevated mortality of adult sockeye salmon (*Oncorhynchus nerka*) during river migration. We show that cardiorespiratory physiology varies at the population level among Fraser River sockeye salmon and relates to historical environmental conditions encountered while migrating. Fish from populations with more challenging migratory environments have greater aerobic scope, larger hearts, and better coronary supply. Furthermore, thermal optima for aerobic, cardiac, and heart rate scopes are consistent with the historic river temperature ranges for each population. This study suggests that physiological adaptation occurs at a very local scale, with population-specific thermal limits being set by physiological limitations in aerobic performance, possibly due to cardiac collapse at high temperatures.

Warming oceans and rivers are affecting fish species worldwide (*1*–*4*). In particular, elevated temperatures in streams and rivers are creating lethal conditions for the migration of Pacific salmon to their spawning grounds, raising conservation concerns for these ecologically, economically, and culturally important fish species (*5*–*7*). Because physiological processes are critical in defining temperature-induced mortality (*8*), we investigated whether thermal limits are set at a local level and by physiological limitations in aerobic performance due to cardiac collapse.

The lifetime fitness of millions of sockeye salmon (*Oncorhynchus nerka*) that annually return to the Fraser River (British Columbia, Canada) depends on a physically demanding upriver migration. During this once-in-a-lifetime event, fish swim continuously against a fast flowing river for several weeks at ground speeds of 20 to 40 km day^{-1} (*9*). Feeding ceases in the ocean, and upriver swimming is fueled entirely by endogenous energy stores. Because sockeye salmon return to natal spawning grounds with remarkable fidelity, the Fraser River is home to more than 100 genetically and geographically distinct populations (*10*), each of which experiences variable upriver migration conditions, depending on when they enter the river and where they spawn. Thus, populations vary in migration distance (100 to 1100 km), elevation gain (10 to 1200 m), river temperature (9° to 22°C), and river flow (2000 to 10,000 m^3 s^{-1}) (Fig. 1B and table S1). Reproductively isolated populations can potentially adapt to the environmental conditions that induce maximal aerobic challenges, which for sockeye salmon likely occur during their upriver spawning migration. Indeed, local migratory conditions apparently exert strong selective pressure for adaptation because morphological and behavioral characteristics (gross somatic energy, body morphology, egg number, and swimming behavior) do correlate with river migration distance, elevation gain, and/or work (distance × elevation gain) in sockeye salmon (*11*, *12*). Therefore, we hypothesize that physiological adaptation in sockeye salmon occurs locally at the population level, reflecting upriver migration conditions.

We apply an established conceptual and mechanistic framework for understanding temperature effects on aquatic ectotherms, the oxygen- and capacity-limited thermal tolerance (OCLTT) hypothesis (*13*–*15*). OCLTT attributes the decline in aerobic scope (the difference between resting and maximal oxygen consumption rates) above an animal's optimal temperature (T_{opt}) to capacity limitations of the organ systems that deliver oxygen to tissues. Here, we focus on heat tolerance, given the prevailing warming trend for the Fraser River (fig. S1). The expectation is that local adaptations should extend to multiple levels of the cardiorespiratory system, explaining intraspecific variation in thermal tolerance and aerobic scope.

Our study included eight populations of wild-caught Fraser River sockeye salmon, spanning

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